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Original Research Article

The complex dynamics of a diffusive prey–predator model with an Allee effect in prey

Feng Rao [a], Yun Kang [b,*]

[a] College of Sciences, Nanjing Tech University, Nanjing, Jiangsu 211816, China
[b] Sciences and Mathematics Faculty, College of Integrative Sciences and Arts, Arizona State University, Mesa, AZ 85212, USA

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ABSTRACT

This paper investigates complex dynamics of a predator–prey interaction model that incorporates: (a) an Allee effect in prey; (b) the Michaelis–Menten type functional response between prey and predator; and (c) diffusion in both prey and predator. We provide rigorous mathematical results of the proposed model including: (1) the stability of non-negative constant steady states; (2) sufficient conditions that lead to Hopf/Turing bifurcations; (3) a prior estimates of positive steady states; (4) the non-existence and existence of non-constant positive steady states when the model is under zero-flux boundary condition. We also perform completed analysis of the corresponding ODE model to obtain a better understanding on effects of diffusion on the stability. Our analytical results show that the small values of the ratio of the prey's diffusion rate to the predator's diffusion rate are more likely to destabilize the system, thus generate Hopf-bifurcation and Turing instability that can lead to different spatial patterns. Through numerical simulations, we observe that our model, with or without Allee effect, can exhibit extremely rich pattern formations that include but not limit to strips, spotted patterns, symmetric patterns. In addition, the strength of Allee effects also plays an important role in generating distinct spatial patterns.

1. Introduction

Prey–predation interactions have been a central theme for ecological studies in the past few decades (Volterra, 1926; Arditi and Ginzburg, 1989; Berryman, 1992; Kuang and Beretta, 1998; Abrams and Ginzburg, 2000; Hsu et al., 2001; Kang and Wedekin, 2013). To study the interaction between predators and their prey, it is important to determine the specific form of the functional response between prey and predator that describes the amount of prey consumed per predator per unit of time since it affects the population dynamics dramatically (Akcakaya et al., 1995). In literature, The Holling-Type II functional response (i.e., prey density dependence) has been considered as a biological meaningful functional response (Li and Kuang, 2007). Some researchers have argued that a functional response depending on the ratio of prey to predator abundance is a suitable representation of some phenomena (Arditi and Ginzburg, 1989). For example, when predators have to search for food (and therefore have to share or compete for food), a more suitable general predator–prey theory such as the ratio-dependent theory (i.e., the per capita predator growth rate of the predator depends on a function of the ratio of prey to predator abundance), should be considered. The work by Akcakaya et al. (1995) and Hsu et al. (2001) supports that the ratio-dependent predation models (also called the prey–predator models with Michaelis–Menten type functional responses) are capable of producing richer and more reasonable dynamics biologically. Among all predator–prey models, the predation systems with the Michaelis–Menten type functional responses have gained a great interest over many decades (a partial list of references may be found in Kuang and Beretta (1998), Hsu et al. (2001), Xu and Chaplain (2002), Wang et al. (2007), Meng et al. (2010), Rao and Wang (2012), Rao (2014) and the references cited therein). However, many of these studies have concentrated on the existence, uniqueness and the stability analysis of predation systems. In addition to the functional response between prey and predator, there are many other factors such as Allee effects, dispersal movements of both prey and predator, contributing greatly to the population dynamics of prey and predator. In this paper, we propose a reaction–diffusion predator–prey model with Allee effects in prey and diffusion in both prey and predator to investigate how the synergy of Allee effects and diffusion affect the spatial temporal dynamics. More specifically, we focus on the rich

* Corresponding author.
E-mail addresses: raofeng2002@163.com (F. Rao), yun.kang@asu.edu (Y. Kang).

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spatial-temporal dynamics of a Michaelis–Menten type prey–predator model that is distinct from others by incorporating (1) an Allee effect in prey (which can be weak or strong); and (2) diffusion in both prey and predator.

In population dynamics, Allee effect refers to the positive correlation between the population density and the per capita growth rate (Stephens et al., 1999), which is introduced by Allee (1978). The Allee effect can be caused by a number of sources such as difficulties in finding mates at small densities, reproductive facilitation, predation, environmental conditioning and inbreeding depressions. Allee effect can be classified into strong and weak cases. The strong one introduces a population threshold, and the population must surpass this threshold to grow. In contrast, a population with a weak Allee effect does not have such threshold. Detailed investigations relating to the Allee effect can be found in the papers (Petrovskii et al., 2002; Kent et al., 2003; Zhou et al., 2005; Shi and Shivaji, 2006; Morozov et al., 2006; Çelik and Duman, 2009; Wang et al., 2011; Kang and Yakubu, 2011; Kang and Castillo-Chavez, 2014).

Allee effect can have a huge impact on the population dynamics (Cai et al., 2014). For example, Petrovskii et al. (2002) showed that a fully deterministic predator–prey model with the Allee effects in prey can predict a patchy invasion under certain the parameter range and the model has interesting dynamical features such as the coexistence state is unstable but no stable limit cycle exists. In Kent et al. (2003), Kent et al. concluded that the predator–prey system can be stabilized by an influx of prey due to a rescue effect, and be destabilized by an outflux of an Allee effect. Zhou et al. (2005) selected two classical predator–prey systems with the Allee effects in both predator and prey populations. They showed that the Allee effect may be a destabilizing force in these predator–prey systems. Çelik and Duman (2009) investigated the impact of the Allee effect (on prey population) on the stability of the positive equilibrium point for a discrete-time predator–prey system. Wang et al. (2011) considered the dynamic of a reaction–diffusion Holling type II predator–prey system with strong Allee effect in the prey population. They showed that the impact of the Allee effect increases the system spatiotemporal complexity. The Allee effect was shown to bring essential changes to the population dynamics and it has drawn considerable attention in almost every aspect of ecology and conservation, however, there is no work that has been done for the spatio-temporal dynamics of Michaelis–Menten type predator–prey model with an Allee effect in prey. One of our main motivations is to study the synergistic effects of Allee effects in prey and diffusion in both species on the prey–predator population dynamics.

Understanding the spatial patterns and the related mechanisms of interacting species has been a great interest in conservation biology and ecology. Theoretically, there are a fair amount work by using two nonlinear reaction–diffusion equations in two spatial dimensions to study the invasion dynamics of predator–prey systems (Lewis and Kareiva, 1993; Morozov et al., 2006; Wang et al., 2011). To understand the role of random mobility of the individuals or organisms on the stability and persistence of interacting species, the diffusive predator–prey models have been studied by many authors (Lin et al., 1988; Murray, 1990; Lou and Ni, 1996; Pang and Wang, 2003; Cantrell and Cosner, 2003; Baurmann et al., 2007; Banerjee and Banerjee, 2012) either qualitatively or numerically. In Lou and Ni (1996), Lou and Ni dealt with a strongly-coupled parabolic prey–predator system. They investigated the effects of diffusion, self-diffusion and cross-diffusion on the dynamics of the system. Baurmann et al. (2007) studied a generalized predator–prey system on a spatial domain where diffusion is considered as the principal process of motion. Banerjee and Banerjee (2012) considered a modified spatiotemporal ecological system originating from the Holling-Tanner model by incorporating diffusion terms with both numerical and analytical approaches.

The diffusion has been observed as causes of the spontaneous emergences of ordered structures, called patterns, in a variety of nonequilibrium situations (Wen, 2013). Patterns generated in homogeneous environments are particularly interesting because they require an explanation based on the individual behavior of organisms, and they emerge from interactions in spatial scales that are much larger than the characteristic scale of individuals (Alonso et al., 2002). In mathematics, pattern formation refers to the process that, by changing a bifurcation parameter, the spatially homogeneous steady states lose stability to spatially inhomogeneous perturbations, and stable inhomogeneous solutions arise (Wang and Hillen, 2007). In recent years, many researchers show that the reaction–diffusion predator–prey model is an appropriate tool for investigating the fundamental mechanism of complex spatiotemporal predation dynamics (see Alonso et al., 2002; Baurmann et al., 2007; Wang et al., 2007; Banerjee and Petrovskii, 2011; Rodrigues et al., 2011 and the references therein). There is a limited work on a reaction–diffusion model with the Michaelis–Menten type functional response incorporating an Allee effect in prey population. In this work, we study a Michaelis–Menten type predator–prey interaction model where random movements of both species are described by the diffusion terms and prey has Allee effects ranging from weak to strong. Our model uses the traditional framework of reaction–diffusion equations where the reaction part follows the Michaelis–Menten type interaction between prey and predator population. We assume that both prey and predator are capable to diffuse over a two dimensional landscape. We aim to answer the following questions through our analytic and numerical results:

1. What are the synergistic effects of diffusion and Allee effects on the spatiotemporal dynamics of our model?
2. Can our proposed model generate distinct spatial patterns? And what are the mechanisms generating these different patterns?

The organization of this paper is as follows. In Section 2, we derive a reaction–diffusion Michaelis–Menten type predator–prey model with an Allee effect in prey. In Section 3, we carry out the analysis of the basic dynamics of the model, and prove a prior estimate for positive steady states of the model. In Section 4, we analyze the stability of non-negative constant steady states, and provide sufficient conditions that guarantee the existence of Hopf/Turing bifurcation at positive constant steady states. For the comparison, we also provide the completed analysis for the corresponding ODE model. In Section 5, we provide sufficient conditions that can lead to the non-existence and existence of non-constant positive steady states. In Section 6, we use numerical simulations to reveal the emergence of different patterns and the influences of diffusion and Allee effects on the dynamical behavior of the model. We conclude our work in Section 7 and the detailed proofs of our theoretical work are given in the last section.

2. Model derivation

The two-dimensional Michaelis–Menten type prey–predator interaction model can be described as follows:

$$\begin{cases} \dfrac{dN}{dT} = F(N) - A\dfrac{NP}{N+P}, \\ \dfrac{dP}{dT} = \mu A\dfrac{NP}{N+P} - MP, \end{cases} \tag{1}$$

where $N(T)$ and $P(T)$ are the population densities of prey and predator at time $T \geq 0$, respectively; A is the predation rate, μ is the

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